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by John Skarha

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Hydrogen is the most abundant element in the universe. Fossil fuel production of hydrogen is based on steam reforming of natural gas, thermal cracking of natural gas, partial oxidation of heavier than naphtha hydrocarbons, coal gasification, and the splitting water with electricity typically generated from carbonaceous fuels. Among these methods, nearly 90% of hydrogen for commercial use is produced by the steam reforming process (Demirbas, 2009, p. 2). These energy-intensive industrial processes typically release polluting by-products such as carbon dioxide and other greenhouse gases. In addition to thermochemical hydrogen production, hydrogen can also be produced biologically. Biohydrogen is the term used to describe hydrogen that is produced from renewable resources such as water, organic waste or biomass, either biologically or photobiologically (Demirbas, 2009, p. 1). When compared to photoelectrochemical or thermochemical processes, biohydrogen production has several advantages due to its low energy requirement and investment cost. In fact, the majority of the biologically produced hydrogen in the biosphere is derived from microbial fermentation processes in which organic matter is decomposed into carbon dioxide and hydrogen (Demirbas, 2009, p. 1).

Hydrogen production using biological methods is based on biophotolysis of water by algae and cyanobacteria, photodecomposition of organic compounds by photosynthetic bacteria, fermentative hydrogen production from organic compounds and hybrid systems using photosynthetic and fermentative bacteria (Demirbas, 2009, p. 166). As described in (Demirbas, 2009, p. 168-169), there are currently two biological pathways that organisms use for hydrogen production. The most common method is through a natural fermentation process and much research in the development of biohydrogen production is based on this approach. However, a big downside to this technique is the production, collection, and delivery of sugar-based biomass sources, which can involve significant, potentially non-renewable, energy expenditure. A more efficient and effective approach is the direct production of biohydrogen that utilizes microorganisms capable of using solar photons to separate oxygen from water.

Biophotolysis is the term used to describe the action of light on a biological system that results in the dissociation of a substrate, usually water, into molecular hydrogen and oxygen. One significant advantage of biophotolysis is that it is an extremely efficient conversion of solar energy to hydrogen. Compared to the 0.2 to 2.6% photosynthetic efficiencies using sugar-based energy crops today, direct hydrogen conversion from sunlight may offer a conversion efficiency of as high as 40% (Demirbas, 2009, p. 165166). Photosynthetic microorganisms, such as cyanobacteria and micro-algae, can produce hydrogen by using the energy of the sun to convert H_2O into H_2 and provide an attractive alternative to fossil fuels (Weyman et al., 2011, p. 1). As described in Weyman et al. (2011), cyanobacteria can produce H_2 using either nitrogenase or hydrogenase enzymes. Hydrogenases may be more efficient for the large-scale production of H_2 as an alternative energy storage molecule, since the process catalyzed by nitrogenases requires ATP (Vargas, Weyman, Tong, Smith, & Xu, 2011, p. 1990).

The role of hydrogenases considered here is to catalyze the reduction of protons to molecular H_2 according to the equation $2H^+ + 2e^- \rightarrow H_2$. In general, a hydrogenase can catalyze either H_2 production to dissipate excess reductant or H_2 oxidation to capture the energy in H_2, depending on

the energy demands of the cell. In addition to the important function of energy metabolism, hydrogenase activity is also involved in other cellular processes, such as methanogenesis, nitrogen fixation, and pathogenesis and microbes may contain one or more hydrogenases that are found in the cytosol, the periplasm, or the cell membrane (Vargas et al., 2011, p. 1990). Typically, hydrogenases are divided into three phylogenetically-distinct categories that correlate with the metal composition of the active site: [FeFe], [NiFe], and the [Fe] hydrogenases (Weyman et al., 2011, p. 1), where the [NiFe] hydrogenase represents the largest known group of the hydrogenases (Vargas et al., 2011, p. 1990). One major difficulty of using a hydrogenase in a photosynthetic organism is that most hydrogenases are typically inhibited by oxygen, which is an inherent byproduct of photosynthesis. This inhibition would thus limit the rate of hydrogen production. As discussed in Vargas et al. (2011), the [FeFe] hydrogenases are the most O_2-sensitive and are usually irreversibly destroyed by exposure to oxygen. Most promising are the [NiFe] hydrogenases which only are temporarily inactivated by O_2. Thus the [NiFe] hydrogenase that is incorporated into the genome of the photosynthetic microbe needs to be thermostable and catalytically active in O_2 for a successful biohydrogen production system (Vargas et al., 2001, p. 1990). As listed in Weyman et al. (2011), there are several [NiFe] hydrogenases from other microorganisms that do maintain activity in the presence of oxygen, including those from Ralstonia eutropha, Rubrivivax gelatinousous, and Alteromonas macleodii. At the catalytic heterodimer core of these [NiFe] hydrogenases, there are two subunits, one large (ca. 60 kDa) and one small (ca. 30 kDa), and these typically require an extensive set of accessory proteins to assemble the active catalytic site (Weyman et al., 2011, p. 1). The presence of these accessory proteins is an additional requirement of the organism receiving the [NiFe] hydrogenase gene in order for the function of the hydrogenase enzyme to be fully activated.

The heterologous expression of O_2-tolerant hydrogenases genes in cyanobacteria is the research activity of scientists in the Bioenergy Research group at the J. Craig Venter Institute (JCVI). The purpose of this research is to produce hydrogen for use as a renewable energy source (Smith & Weyman, 2011). An important part of the effort to construct biophotolytic systems is the search for novel O_2-tolerant [NiFe] hydrogenases from environmental microbes (Maroti et al., 2009, p. 5821). As mentioned in Maroti et al. (2009), the oceans harbor an abundance of microorganisms with H_2 production capability. An emerging, rapidly growing field is metagenomics, which enables information to be obtained about uncultured microbes using their raw environmental DNA and allows understanding of the true diversity of microbes in their natural habitats. As such, metagenomics analysis provides a completely new approach for identifying enzymes involved in hydrogen metabolism from the oceans in a culture-independent manner (Maroti et al., 2009, p. 5821). As described in Maroti et al. (2009), the Global Ocean Sampling (GOS) expedition has identified novel [NiFe] hydrogenases and produced the largest metagenomic data sample so far, providing a rich catalog of proteins and protein families. The genes for these hydrogenases have to be heterologously expressed in culturable foreign hosts for protein and functional analyses because source organisms for metagenomic sequences are not typically known. This has been done using the organism T. roseopersicina as a foreign host since it carries the homologous hydrogenase HynSL gene and already has the necessary machinery required to process the environmental hydrogenase (Maroti et al., 2009, p. 5822).

Another experiment was focused on the identification of [NiFe] hydrogenase from Alteromonas macleodii, which is a marine, heterotrophic, gammaproteobacterium and has examined its O_2 tolerance, thermostability, and catalytic activity (Weyman, Smith, & Xu, 2011, p. 1). This organism is globally distributed, but sequence analysis of ribosomal and housekeeping genes indicates that isolates obtained from the Mediterranean Sea at depths between 1000 and 3500 meters are genetically distinct from their surface-isolated counterparts (Weyman, Smith, & Xu, 2011, p. 1). As presented in Weyman, Smith, & Xu (2011), when the sequenced genomes of representative deep ecotype (AltDE) and surface ecotype (ATCC 27126) strains of A. macleodii were compared, many

differences were identified, including the presence of a [NiFe] hydrogenase in AltDE, but not in ATCC 27126. It was found that the [NiFe] hydrogenase gene locus was present in a 95-kb gene island and it included the hynS and hynL genes, which encode the hydrogenase small and large subunits, respectively, and the genes predicted to encode the accessory proteins that are responsible for maturation of the hydrogenase. The AltDE hydrogenase gene was subsequently inserted into T. roseopersicina and was found to be active (Weyman, Smith, & Xu, 2011, p. 1). The researchers speculate that the presence of this hydrogenase in AltDE helped the original host organism survive in the nutritionally depleted environment of the dark depths of the Mediterranean Sea.

Regarding the target market, since it generates only water as a byproduct, biohydrogen is an environmentally friendly alternative to gasoline that can be used in an internal combustion engine. Due to its environmental merits, it is expected that the share of biohydrogen in the automotive fuel market will grow rapidly in the next decade (Demirbas, 2009, p. 163). In addition, the clean burning of biohydrogen within a fuel cell is a general-purpose energy resource that can provide basic energy services that are fundamental to a modern economy. These include the heating, cooling, and lighting of buildings, powering industrial processes, processing food, fueling transport, and energizing communications and information technologies (Demirbas, 2009, p. 2).

The current world energy supply system is facing three significant problems: (1) limited fossil fuel resources, (2) climate change by carbon dioxide emission, and (3) insecurity by nuclear weapon competence and radioactive materials. Additionally, another problem with petroleum fuels is their uneven distribution throughout the world, with the Middle East having 63% of the global reserves and being the dominant supplier of petroleum (Demirbas, 2009, p. 5). These supply, distribution, environmental, economic, and geopolitical concerns have far-reaching implications, leading to the conclusion that the current energy system is unsustainable. One possible solution to all of these problems is the biophotolytic production of sustainable and renewable hydrogen by microbes. Hydrogen is the ideal energy carrier for the future since it is storable, transferable, has minimal environmental impact, has high heat value per mass unit, and its sources are globally distributed (Demirbas, 2009, p. 1). Of course, much work remains to be done to demonstrate the viability of using hydrogenase genes in photosynthetic organisms to produce biohydrogen and deliver this resource to a wide range of commercial applications. However, the future is bright for this biotechnology to be a long-term energy solution.

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